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TREE CROWN STRUCTURE AND VASCULAR EPIPHYTE DISTRIBUTION IN *SEQUOIA SEMPERVIRENS* RAIN FOREST CANOPIES

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ABSTRACT. Crown structure and vascular epiphytes were studied in eight large (82–97 m tall, 3.3–7.2 m dbh) redwood trees (*Sequoia sempervirens*) in old-growth temperate rain forests, using rope-based methods of access. The trees had complex individualized crowns consisting of multiple (12–62 per tree) reiterated trunks arising from other trunks and branches. Trunk-to-trunk and trunk-to-branch fusions were common, and the diameter of a trunk above a fusion was often greater than below the fusion. Thirteen species of vascular plants, including a spike-moss, three ferns, four shrubs, and five trees, grew as epiphytes. Many of the species were accidental epiphytes whose primary habitat was the forest floor. They grew in deep humus accumulations on large branches and in crotches formed by multiple trunks. Three species dominated epiphyte assemblages. The deciduous fern *Polypodium glycyrrhiza* was abundant on two of the trees, where it was always restricted to lower crowns. The evergreen fern *Polypodium scouleri,* the most abundant vascular epiphyte, occurred in the upper and lower crowns of all eight trees. The ericaceous shrub *Vaccinium ovatum* also occurred on all eight trees but was abundant on only four trees with large quantities of decaying wood in their crowns. *Polypodium* ferns were more frequent on living branches, while ericaceous shrubs were more frequent on trunks and dead branches. Complex crown structure clearly promoted humus accumulation and vascular epiphyte abundance, but much of the tree-to-tree variation in epiphyte distribution was attributed to differences in tree age, stand-level microclimate, tree health, and dispersal limitations.

Key words: epiphytes, redwoods, *Sequoia sempervirens,* temperate rain forest

INTRODUCTION

Tall conifers dominate temperate rain forests in western North America. Young conifers in these forests exhibit a characteristic architecture: one large, orthotropic (i.e., vertically oriented) trunk supporting numerous smaller, more or less plagiotropic (i.e., horizontally oriented) branches. Trees growing in sheltered forests may retain this simple crown structure well into old age. Branches in the lower portion of conifer crowns frequently are lost by self-pruning, especially in shade-intolerant species. Thus, the lower trunks of tall trees in old-growth forests are typically free of branches for 20 m or more (Franklin et al. 1981, Kuiper 1988, Stewart 1989).

Disturbances (e.g., treefalls) that increase light availability can lead to dramatic changes in tree crown structure (Hallé et al. 1978, Oldeman 1990). Epicormic branches, which appear as fan-shaped arrays (Pike et al. 1977), can sprout from well-illuminated conifer trunks long after the original branches have been lost. Main trunks of tall conifers that snap in severe storms often sprout new trunks. Even branches receiving abundant light can sprout orthotropic stems that can be considered new trunks. These trunks are, in effect, reiterations of the tree's architectural model (Hallé et al. 1978), with each one supporting its own system of plagiotropic branches. Thus, a reiterated trunk is indistinguishable from a free-standing tree except for its location within the crown of a larger tree. Few studies of crown structure in tall-stature conifer forests are based on in situ sampling. Most canopy research in these forests has focused on organisms inhabiting tree crowns, especially epiphytes.

Rain forests of western North America harbor large quantities of epiphytes, whose biomass can exceed several metric tons per ha (Nadkarni 1984, McCune 1993). Epiphytes of old-growth forests dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae) (hereafter Douglas-fir forests) have been studied for nearly three decades (Sillett & Neitlich 1996). These forests support an abundance of epiphytic lichens and bryophytes (Pike et al. 1975). Only one species of vascular plant, the fern *Polypodium glycyrrhiza* D.C. Eaton (Polypodiaceae), regularly occurs epiphytically in the canopy. It is associated with thick bryophyte mats on branches (Sillett 1995). Epiphyte assemblages in the oldest, wettest Douglas-fir forests are dominated by bryophytes and vascular plants, including a number of accidental epiphytes whose primary habitat is terrestrial (Sillett & Neitlich 1996). Little is known about canopy structure or epiphyte assemblages in western forests not dominated by Douglas-fir.

The tallest forests in North America are dominated by *Sequoia sempervirens* (D. Don) Endl. (Cupressaceae) (hereafter redwood). These for-

TABLE 1. Locations and dimensions of the eight redwood trees in the study. Trees 1–4 were in Prairie Creek Redwoods State Park, and Trees 5–8 in Jedediah Smith Redwoods State Park.

Tree	Total height (m)	DBH (m)	No. of reiterated trunks	Wood volume (m^3) Main trunk	All reiterations	Largest reiteration
1	95.8	3.31	61	234.8	20.9	4.4
2	97.0	3.69	55	260.3	4.0	1.4
3	82.5	3.47	62	290.5	16.1	2.1
4	88.6	7.10	21	649.3	113.5	33.1
5	85.7	4.58	23	349.9	35.3	28.9
6	93.0	3.93	12	370.5	10.5	3.4
7	86.7	5.35	26	471.1	15.8	3.5
8	93.7	7.23	43	945.6	99.1	46.4

ests harbor the tallest known living trees (Carder 1995). Individual redwood trees can reach 112 m in height (Sawyer et al. 1999). These are the most massive forests on Earth. Individual forest stands can have a wood volume of more than 10,000 m^3 per ha and a biomass of more than 3000 metric tons per ha (Sawyer et al. 1999). The canopy structure of these impressive forests has been unexplored except for a single unpublished ground-based study (Mulder & de Waart 1984). There are no publications on epiphytes in redwood forests.

I initiated the first in situ studies of redwood forest canopies in 1996 at Humboldt State University. My rope-based research has focused on canopy structure and epiphyte distribution in old-growth redwood forests. This study had two specific objectives: 1) to describe crown structure of eight large redwoods and 2) to assess distribution and abundance of vascular epiphytes in these tree crowns.

STUDY AREA

This study focused on four old-growth forest stands between 50 and 100 m elevation. Three stands are located in Prairie Creek Redwoods State Park (PCRSP), Humboldt County, California. Mean annual rainfall in PCRSP is 1.75 m; summer temperatures range from 4 to 24°C; and winter temperatures range from −1 to 13°C (Redwood National and State Parks). One stand is located in Jedediah Smith Redwoods State Park (JSRSP), Del Norte County, California. Mean annual rainfall in JSRSP is 2.5 m; summer temperatures range from 7 to 29°C; and winter temperatures range from −1 to 16°C (Redwood National and State Parks). Both Parks experience a summer dry season ameliorated by persistent fog. Stands have basal areas between 270 and 370 m^2 per ha. In two stands along Godwood Creek in PCRSP, redwood accounts for 75% of the basal area with co-dominant *Picea sitchensis* (Bong.) Carrière up to 90 m tall forming most of the remainder. In the other two stands, redwood accounts for 90% of the basal area. All stands contain small amounts of *Tsuga heterophylla* (Raf.) Sarg. (Pinaceae) as well as *Lithocarpus densiflorus* (Hook. & Arn.) Rehder (Fagaceae) and/or *Umbellularia californica* (Hook. & Arn.) Nutt. (Lauraceae) in the lower canopy. Understory vegetation is dominated by *Polystichum munitum* (Kaulf.) C. Presl (Aspidiaceae) and *Vaccinium ovatum* Pursh with smaller amounts of *V. parvifolium* Sm. (both Ericaceae), *Rubus spectabilis* Pursh (Rosaceae), *Rhamnus purshiana* DC. (Rhamnaceae), and/or *Acer circinatum* Pursh (Aceraceae). I selected eight large redwoods from the four stands for detailed study (TABLE 1). Trees 1 and 2 grow side-by-side in the same stand along Godwood Creek in PCRSP. Trees 5, 6, 7, and 8 grow in the same stand along Mill Creek in JSRSP.

METHODS

To access tall tree crowns, I shot a rubber-tipped fiberglass arrow trailing 10 kg test strength Fireline® filament over sturdy branches with a powerful compound hunting bow (vertical range = 80 m) mounted to a spinning reel. A 3 mm nylon cord, followed by 11 mm static kernmantle rope, was then hauled over the branches. I anchored one end of the rope at ground level and climbed the other using mechanical ascenders. I used a 20 m long arborist's rope lanyard fitted with a double-end, split-tail system (Sherrill Inc. 1997, see also Jepson 1998) to access progressively higher branches and to move laterally through tree crowns. A rescue pulley was secured near the top of each tree with a tubular nylon webbing sling. The climbing rope was lowered from the tree on nylon cord at the end of the day, and the pulley was used to haul the rope back into place for subsequent ascents via single rope technique.

TABLE 2. Summary of product-moment correlation coefficients (r) between crown structure variables for reiterated trunks on eight redwood trees. Broken reiterations ($N = 47$) were excluded from correlations for total length. Statistically significant correlations ($P < 0.01$) are highlighted in bold. Samples sizes are indicated in parentheses.

	Height of origin	Total length			
All reiterated trunks ($N = 298$)					
Total length	**−0.24**				
Basal diameter	**−0.20**	**0.91**			
	Origin height	Total length	Distance from main trunk	Basal diameter	Branch basal diameter
Reiterated trunks arising from branches ($N = 149$)					
Total length	−0.16				
Distance from main trunk	**−0.36**	0.06			
Basal diameter	−0.11	**0.94**	−0.01		
Branch basal diameter	**−0.26**	**0.63**	0.18	**0.65**	
Branch diameter at reiteration	−0.12	**0.78**	−0.07	**0.82**	**0.75**

Crown Mapping

I mapped the crown structure of each tree by measuring heights, diameters, and distances between reiterated trunks. Numbered aluminum tags were attached to major trunks at 5 m intervals with 2 cm paneling nails. These tags served as benchmarks for height measurements of smaller trunks, branches, and epiphytes. Aluminum tags were also used to label individual trunks for future reference. I recorded the following data for each reiterated trunk: top height, height of origin, basal diameter, and diameter at 5 m intervals along the length of the trunk. For reiterated trunks arising from branches, I also recorded horizontal distance to main trunk, branch height, branch basal diameter, and branch diameter at reiteration. Trunks were referenced to each other by recording azimuths and distances between them at 5 m height intervals. Measurements were made with the aid of a compass, clinometer, and graduated fiberglass tape. Since large trunks often gave rise to complex arrays of smaller trunks, I sketched crown structure and noted physical connections between trunks and branches and whether trunks were monopodial, sympodial, or otherwise broken. The information was used to generate tree crown diagrams via DeltaGraph® and ClarisDraw® software for the Macintosh® computer.

Epiphyte Sampling

I used nondestructive methods to measure sizes and locations of all vascular epiphytes occurring in each tree crown. For each fern mat, I measured five size variables: 1) number of living fronds, 2) maximum frond length, 3) maximum frond order (i.e., rows of pinnae per frond), 4) mat length, and 5) mat width. Four size variables were measured for each shrub: 1) number of stems, 2) maximum stem basal diameter, 3) total length, and 4) maximum crown width. Similarly, I measured trunk basal diameter, total length, and maximum crown width for epiphytic trees. In addition to variables describing epiphyte size, I measured height above ground, distance and azimuth to main trunk, and diameter of supporting branch beneath epiphyte (if present). I also recorded crown locations for individual epiphytes by noting whether they occurred on branches, on trunks, or in crotches at the bases of multiple trunks.

Data Analysis

Wood volume of each tree was calculated by applying two equations to the trunk diameter data. I applied the equation for a parabolic frustum (volume = length/2*[A1 + A2], where A1 and A2 are the upper and lower trunk cross sectional areas) to reiterated trunks and upper sections of the main trunk that tapered rapidly. I used the equation for a regular conic frustum (volume = length*π/3*[lower diameter^2 + (lower diameter)*(upper diameter) + upper diameter^2]) for sections of the main trunk that tapered slowly (R. Van Pelt pers. comm.).

I used linear regression analysis to explore relationships between variables measured during crown mapping and epiphyte sampling. Correlations between crown structure variables were evaluated separately for all reiterated trunks and for the subset of reiterated trunks arising from branches. Correlations between epiphyte variables were evaluated separately for the three dominant epiphyte species (see RESULTS). I tested for associations between these species and crown locations by using the $R \times C$ test of independence (Sokal & Rohlf 1995: 738), where $R = 3$ epiphyte species, and $C = 3$ crown lo-

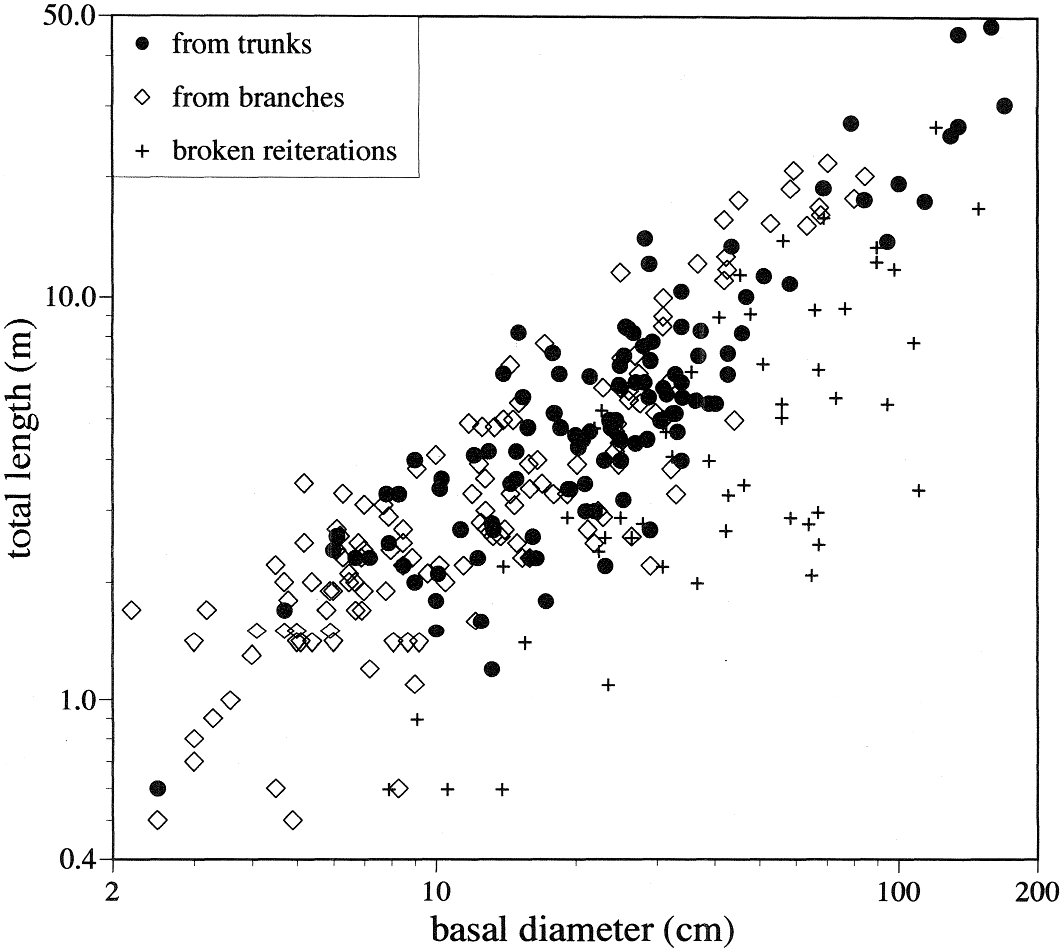

FIGURE 1. Relationship between total length and basal diameter of reiterated trunks in the crowns of eight large redwood trees.

cations. I used G divided by William's correction factor as the test statistic.

I divided the three dominant epiphyte species into size classes using an unweighted ranking procedure. For each species, individual epiphytes were separately ranked in descending order according to each size variable. An average rank was then calculated for each individual, which served as the best estimate of the plants' relative sizes. Ranked lists of epiphytes were then divided into four size classes: first decile (hereafter huge), remainder of the upper third (hereafter large), middle third (hereafter medium), and lower third (hereafter small). Associations between epiphyte size classes and crown locations were tested by using the $R \times C$ test of independence (Sokal & Rohlf 1995: 738), where $R = 4$ size classes, and $C = 3$ crown locations. Again, I used G divided by William's correction factor as the test statistic.

RESULTS

Crown Structure

The eight redwoods had between 12 and 62 reiterated trunks per crown (TABLE 1). I measured a total of 298 reiterated trunks, 149 of which arose from branches. Several significant relationships were evident among crown structure variables (TABLE 2). Larger trunks tended to occur lower in the crown; total length and basal diameter of trunks were negatively correlated with height of origin. Reiterated trunks arising from outer branches were more prevalent in the lower crown; distance from main trunk was neg-

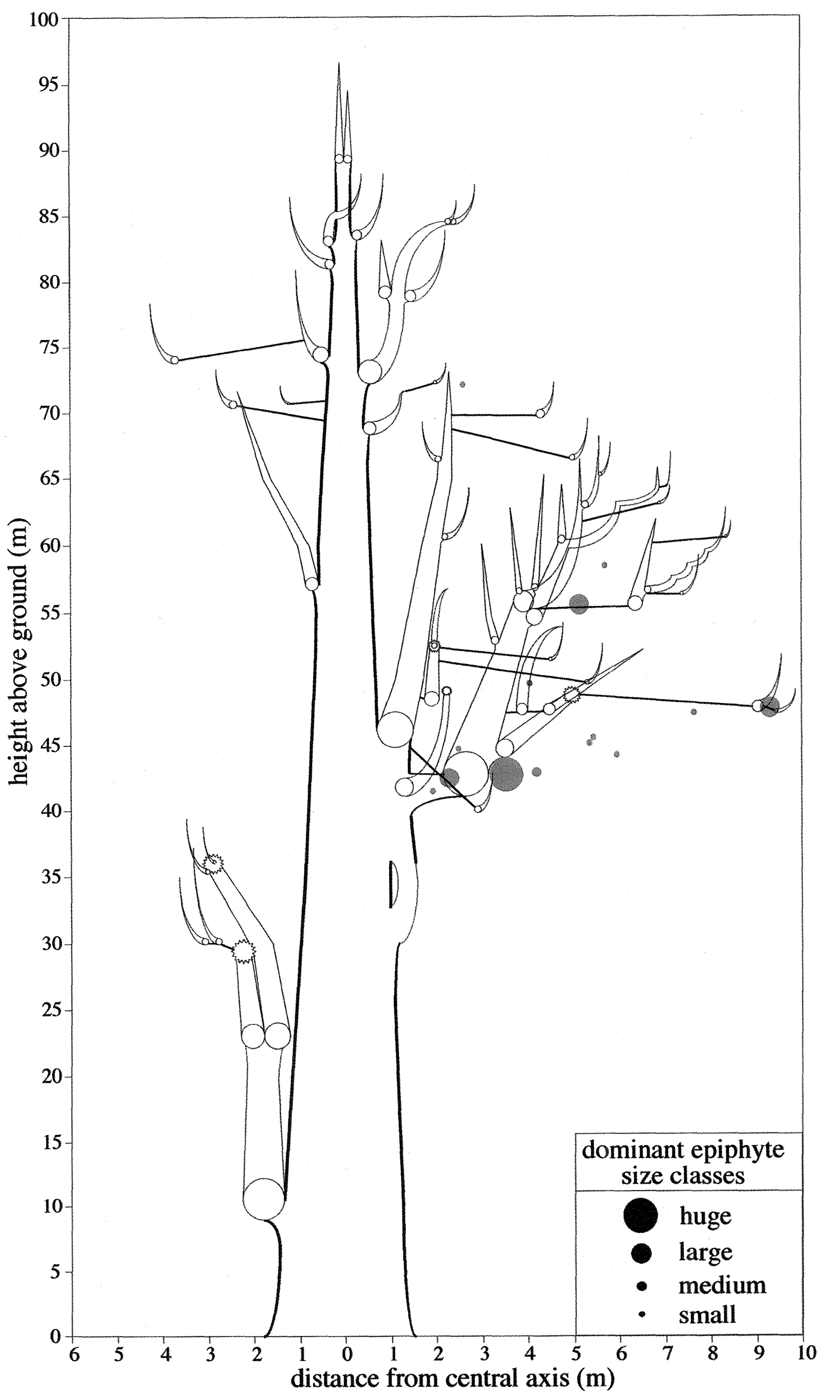

FIGURE 2. Crown structure and vascular epiphytes of redwood Tree 1, Yang, Prairie Creek Redwoods State Park, California. All trunk diameters are drawn to the scale of the x-axis, which is expanded relative to the scale of the y-axis. Circles correspond to the basal diameters of reiterated trunks. Circles with serrated edges indicate broken trunks. Branches bearing reiterated trunks are depicted with single straight lines unless they are more than 1.4 m in basal diameter (see right side of main trunk around 42 m). No other branches, including those supporting "floating" epiphytes, are shown. Colored circles indicate dominant epiphyte species as follows: orange = *Polypodium glycyrrhiza,* green = *Polypodium scouleri,* blue = *Vaccinium ovatum.* Circle sizes correspond to epiphyte size classes (see RESULTS).

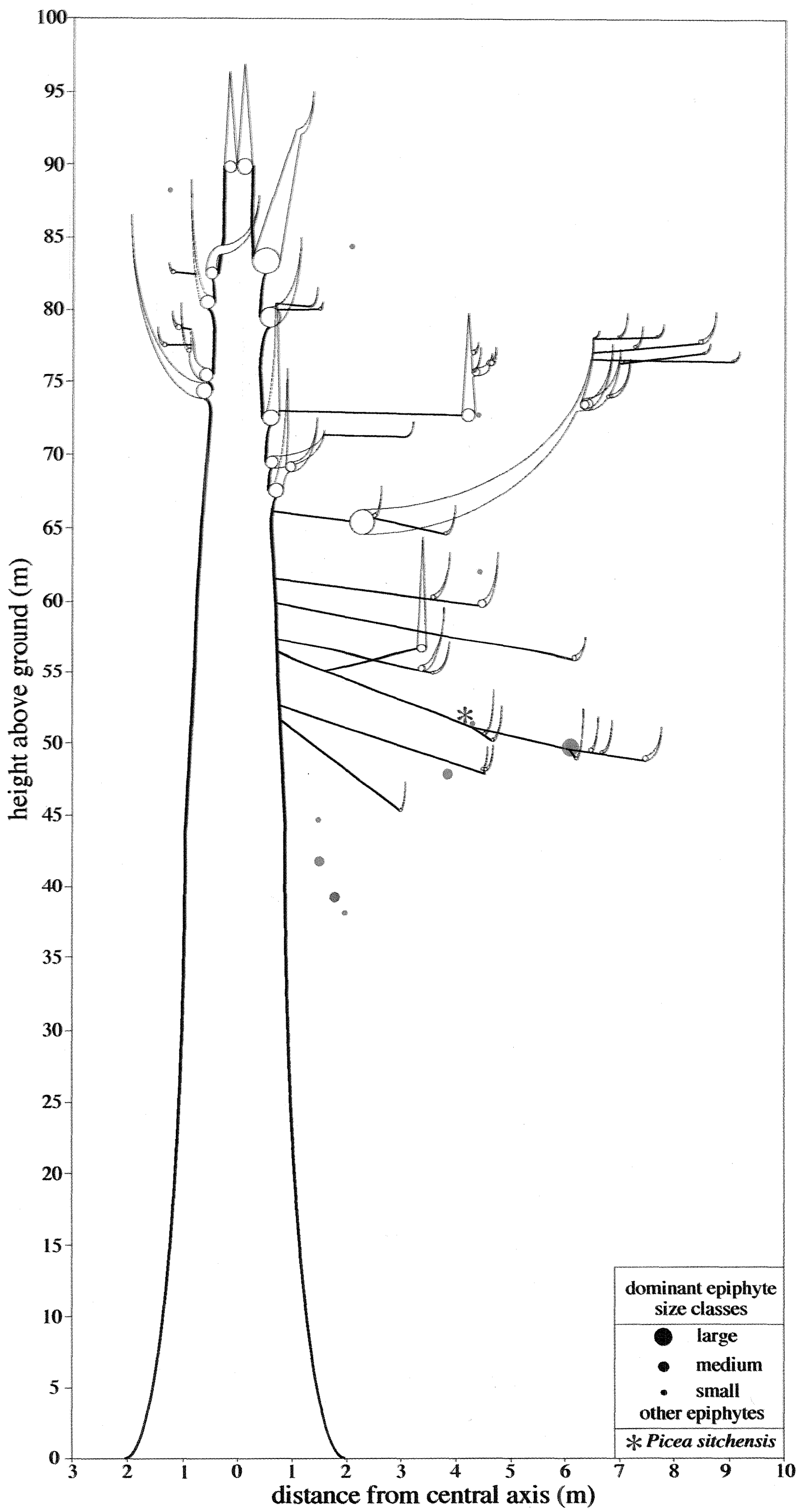

FIGURE 3. Crown structure and vascular epiphytes of redwood Tree 2, Yin, Prairie Creek Redwoods State Park, California (see FIGURE 2 caption).

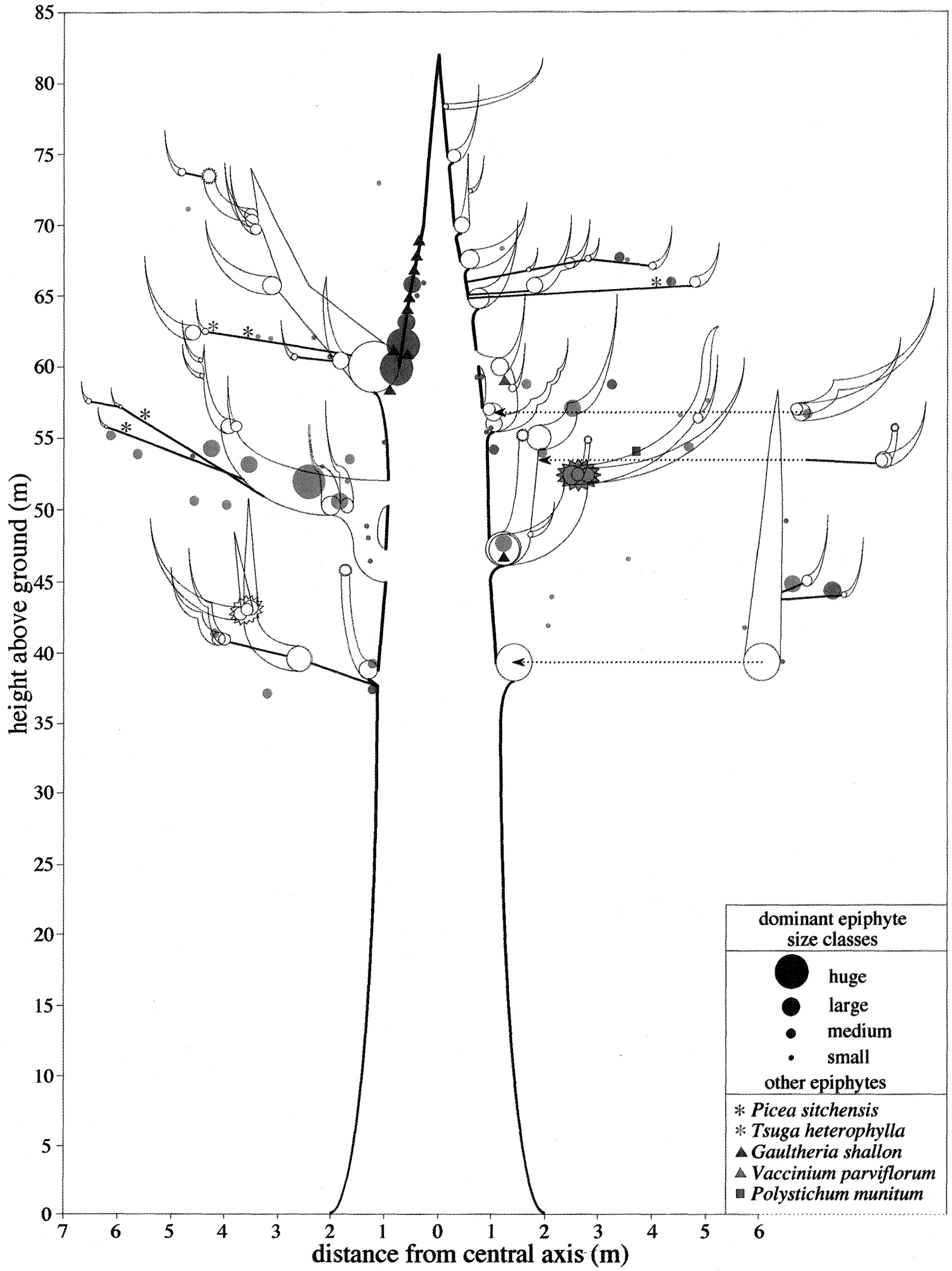

FIGURE 4. Crown structure and vascular epiphytes of redwood Tree 3, Floating Raft Tree, Prairie Creek Redwoods State Park, California. Arrows with dotted lines indicate origins of reiterations that were graphically displaced to the right for clarity (see FIGURE 2 caption).

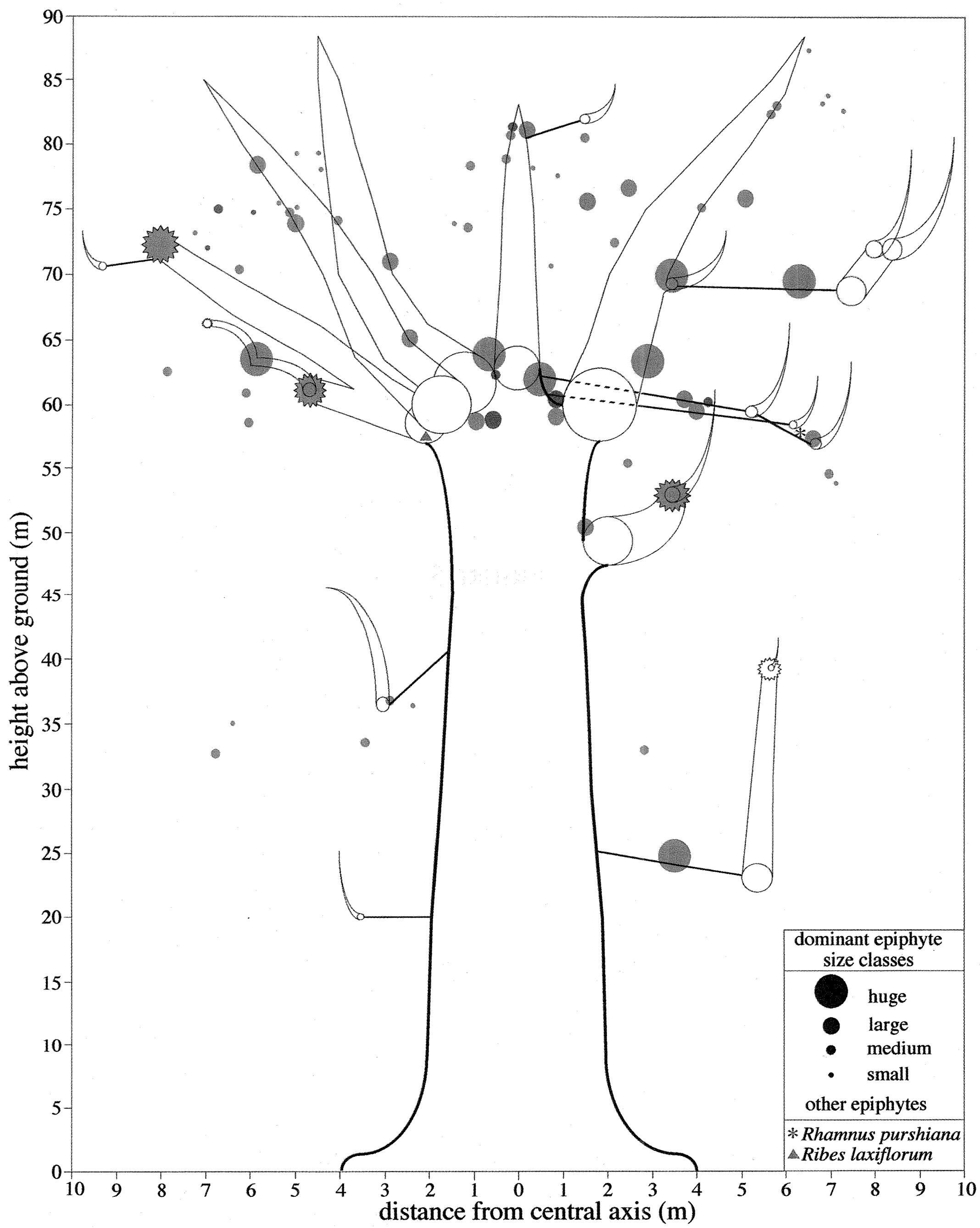

FIGURE 5. Crown structure and vascular epiphytes of redwood Tree 4, Atlas Tree, Prairie Creek Redwoods State Park, California (see FIGURE 2 caption).

atively correlated with height of origin. Thicker branches supporting trunks were more prevalent in the lower crown; branch basal diameter was negatively correlated with height of origin. Thicker branches supported larger trunks than thinner branches; branch basal diameter and branch diameter at reiteration were positively correlated with total length and basal diameter of trunks. Finally, trunk basal diameter was strongly correlated with total length, especially

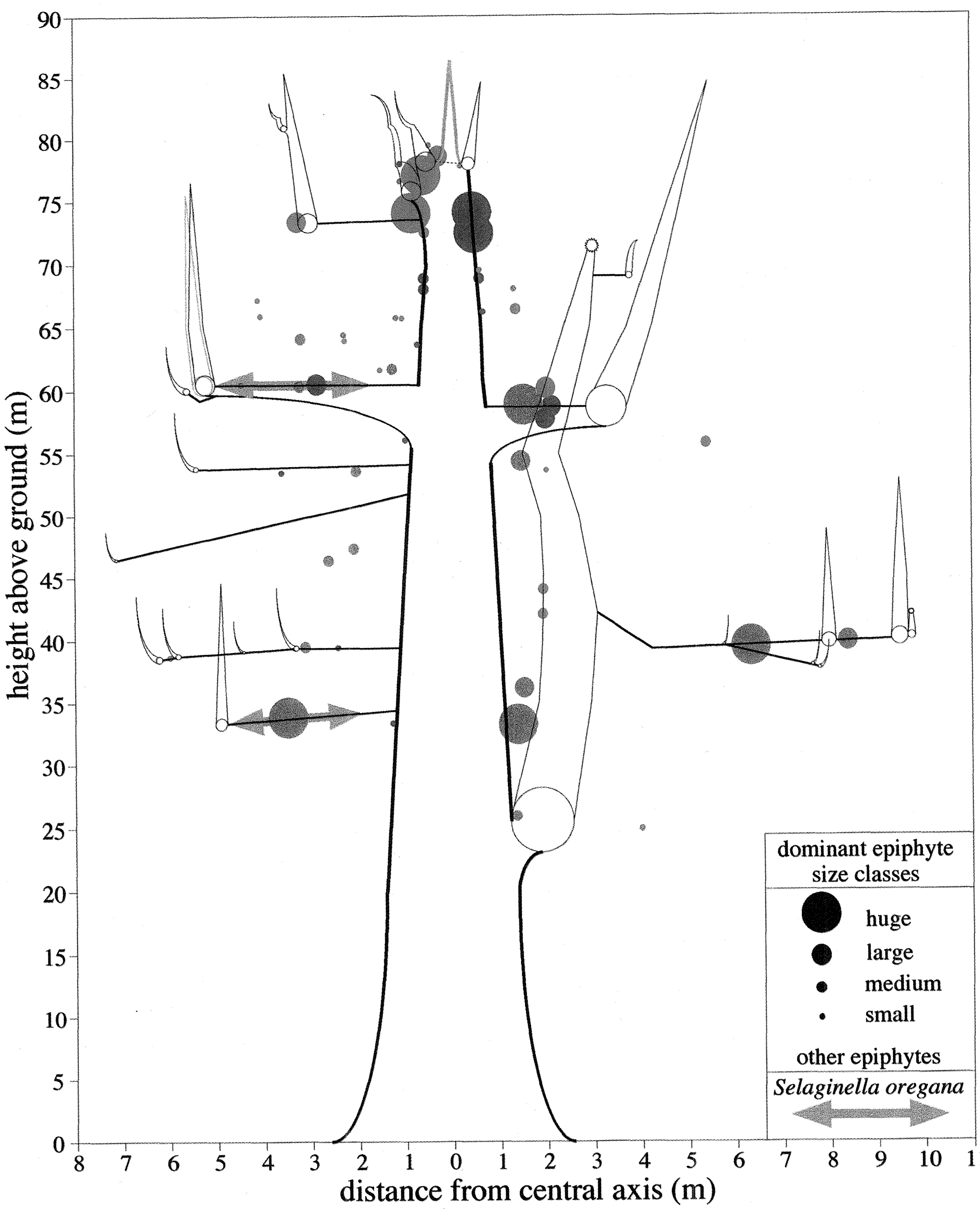

FIGURE 6. Crown structure and vascular epiphytes of redwood Tree 5, Aragorn, Jedediah Smith Redwoods State Park, California. Gray lines indicate dead trunks (see FIGURE 2 caption).

after removing broken trunks from the analysis (TABLE 2, FIGURE 1). Redwood crown structure differed dramatically from one tree to the next, even if they grew side-by-side in the same stand.

Tree 1. The 61 reiterated trunks on Tree 1, including five broken and two sympodial trunks (FIGURE 2), accounted for 8.2% of its total wood volume (TABLE 1). Two massive trunks 0.8 and 1.0 m in basal diameter arose from the right side of the main trunk at 42–46 m and extended into the canopy gap above Godwood Creek. The larger of these trunks supported 20 trunks of its

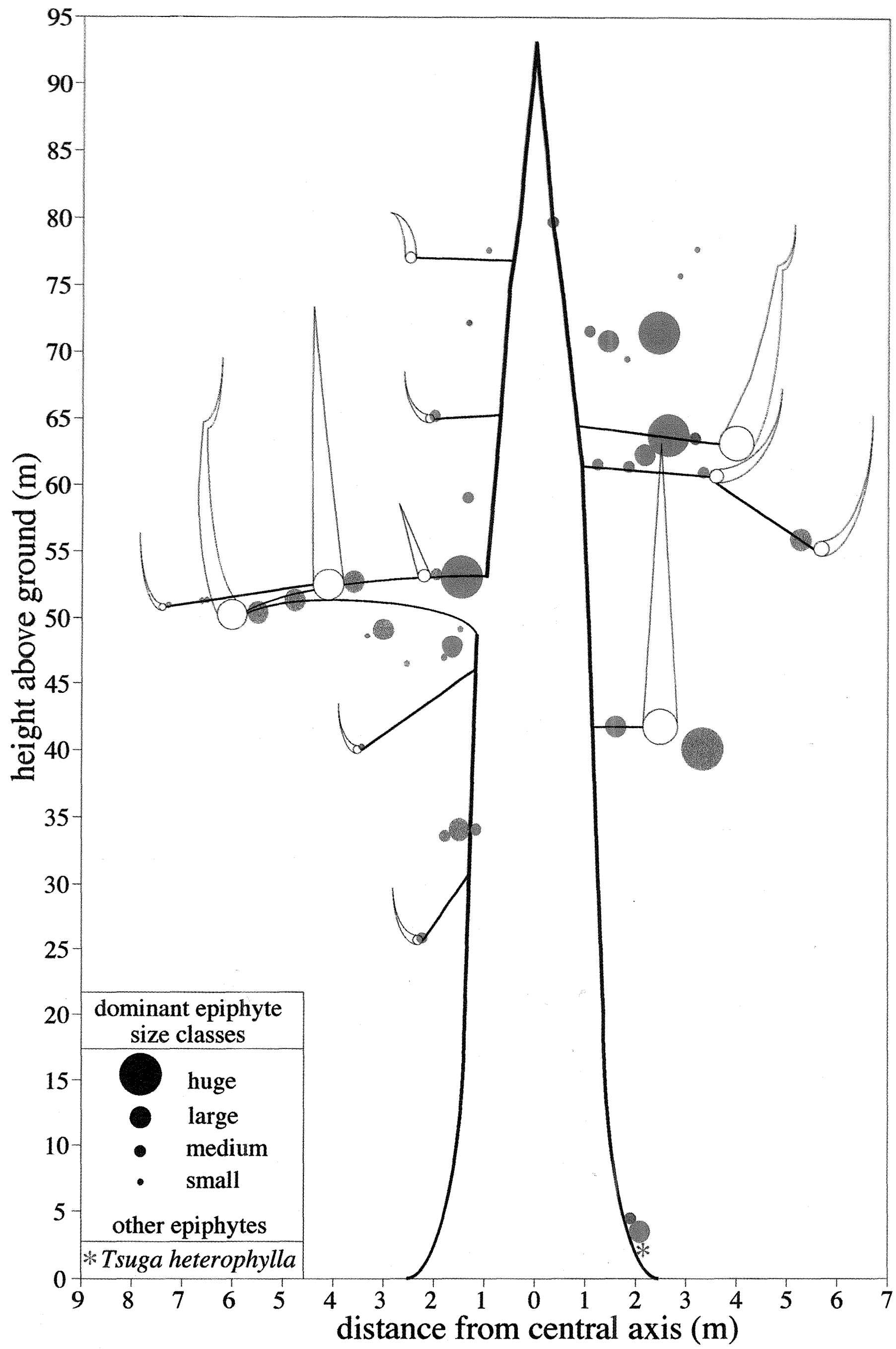

FIGURE 7. Crown structure and vascular epiphytes of redwood Tree 6, Aldebaran, Jedediah Smith Redwoods State Park, California (see FIGURE 2 caption).

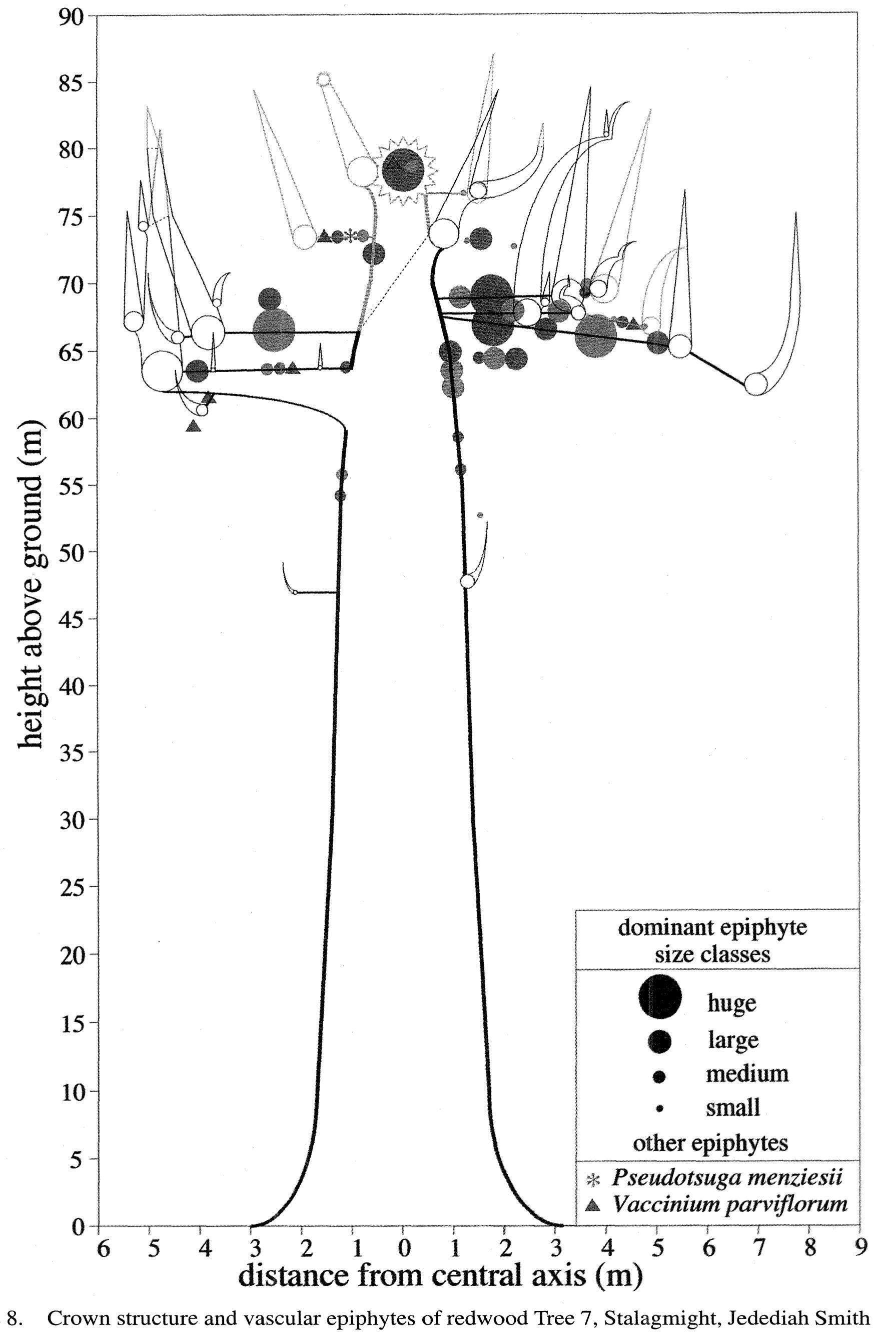

FIGURE 8. Crown structure and vascular epiphytes of redwood Tree 7, Stalagmight, Jedediah Smith Redwoods State Park, California. Gray lines indicate dead trunks and branches (see FIGURE 2 caption).

own, including one with foliage located as far as 10 m away from the main trunk. This enormous reiterated complex arose from a 1.6 m diameter branch that in turn emerged from a region of the main trunk fused with another reiteration originating from the main trunk 10 m below the branch. This fused trunk gave rise to the 0.8 m diameter trunk mentioned above. Note that the diameter of this trunk above the fusion was larger than the basal diameter of the original reiteration. A 0.9 m diameter trunk arose from the left side of the main trunk 10 m above the

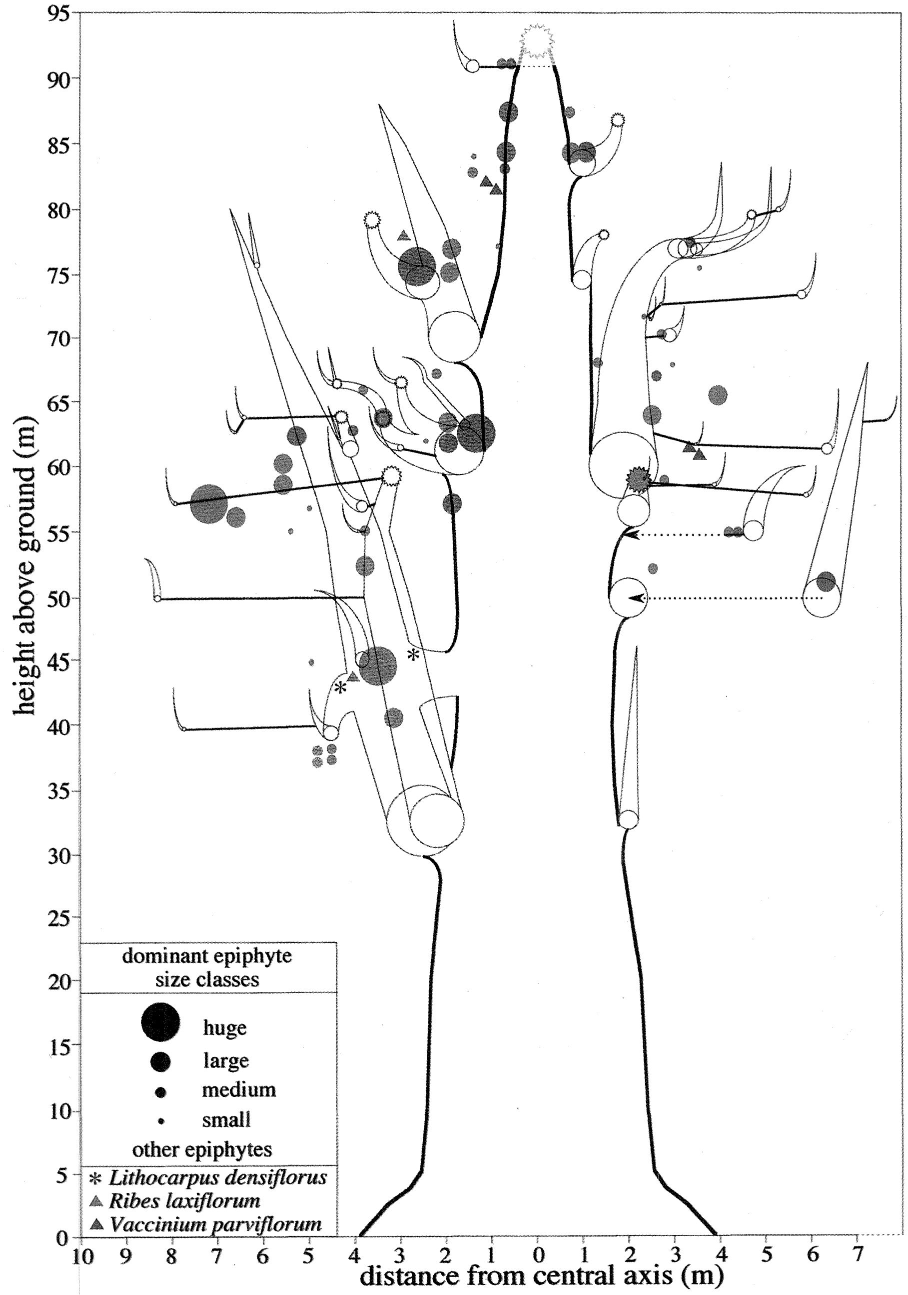

FIGURE 9. Crown structure and vascular epiphytes of redwood Tree 8, Del Norte Titan, Jedediah Smith Redwoods State Park, California. Gray lines indicate dead trunk. Arrows with dotted lines indicate origins of reiterations that were graphically displaced to the right for clarity (see FIGURE 2 caption).

ground. This trunk supported six other trunks, two of which were snapped and resprouting.

Tree 2. The 55 reiterated trunks on Tree 2 (FIGURE 3) accounted for 1.5% of its total wood volume (TABLE 1). Most of its reiterations were oriented away from neighboring Tree 1. Several reiterated trunks arose from the main trunk above 65 m in the crown, and a few of these supported other trunks. Several trunks were fused together on the right side of the main trunk

TABLE 3. Summary of vascular epiphytes occurring in the crowns of the eight redwood trees surveyed in this study. Mean values for epiphyte size are listed along with one standard error in parentheses.

Epiphyte	No. of trees	No. of individuals	Epiphyte size (cm) Length	Width	Description
ERICACEAE					
Gaultheria shallon Pursh	1	9	126 (24.0)	148 (37.3)	Evergreen shrub; common in the understory
Vaccinium ovatum Pursh	8	92	121 (10.4)	123 (11.1)	Evergreen shrub; common in the understory
Vaccinium parvifolium Sm.	3	11	133 (27.4)	69 (11.7)	Deciduous shrub; common in the understory
FAGACEAE					
Lithocarpus densiflorus (H. & A.) Rehd.	1	2	42 (17.5)	15 (5.0)	Evergreen broad-leaved tree; common in the lower canopy
PINACEAE					
Picea sitchensis (Bong.) Carr.	2	4	41 (18.0)	28 (9.5)	Evergreen coniferous tree up to 93 m tall; strictly coastal
Pseudotsuga menziesii (Mirb.) Franco	1	1	15	10	Evergreen coniferous tree up to 100 m tall
Tsuga heterophylla (Raf.) Sarg.	2	3	85 (27.5)	71.7 (10.9)	Evergreen coniferous tree up to 75 m tall
RHAMNACEAE					
Rhamnus purshiana DC.	1	1	100	55	Broad-leaved deciduous tree; common in the understory
SAXIFRAGRACEAE					
Ribes laxiflorum Pursh	2	3	39 (25.0)	128 (64.5)	Deciduous shrub; rare in the understory
PTERIDOPHYTES					
Polypodium glycyrrhiza D.C. Eaton	6	41	67 (7.0)	40 (4.3)	Predominantly epiphytic deciduous fern; strongly associated with bryophytes
Polypodium scouleri Hook. & Grev.	8	212	100.8 (7.1)	55 (4.8)	Predominantly epiphytic evergreen fern; the most abundant vascular epiphyte in redwood rain forests; strictly coastal
Polystichum munitum (Kaulf.) Presl.	1	1	20	10	Evergreen fern; abundant in the understory
Selaginella oregana D.C. Eaton	1	2	300 (20.0)	105 (25.0)	Predominantly epiphytic spike-moss; pendulous epiphyte of temperate rain forests

between 67 and 70 m and 78 and 81 m (not shown in FIGURE 2). Many reiterated trunks arose from branches in the lower half of the crown. The largest of these extended out into a canopy gap and supported 13 trunks of its own, including one with foliage located as far as 9 m away from the main trunk.

Tree 3. The extremely complex crown of Tree 3 had 62 reiterated trunks, including seven broken and six sympodial trunks (FIGURE 4), which accounted for 5.3% of its total wood volume (TABLE 1). The largest of these trunks arose from the main trunk at 60 m and was nearly 1 m in basal diameter. It supported nine trunks of its own, including one that arose from a branch emerging from the broken end of another trunk at 74 m. Several trunks arose from long branches in the middle portion of the crown. Two trunks were fused with other trunks. On the left side of the main trunk at 45 m, a 0.7 m diameter trunk arose from the main trunk and was fused with the base of a 0.9 m diameter trunk at ca. 50 m. With the top of the upper trunk covered with an enormous fern mat, the precise origin of

TABLE 4. Summary of product-moment correlation coefficients (r) between distribution and size variables for the epiphytic fern, *Polypodium scouleri,* on eight redwood trees. Statistically significant correlations ($P < 0.01$, $N = 212$) are highlighted in bold. Correlations for branch diameter are based on smaller sample sizes because 43 ferns did not grow on branches but grew directly on trunks.

	Height above ground	Branch diameter	Distance to main trunk	Number of fronds	Mat length	Mat width	Maximum frond order	Maximum frond length
Branch diameter	−0.01							
Distance to main trunk	**−0.26**	−0.11						
Number of fronds	0.05	**0.41**	−0.09					
Mat length	−0.01	**0.53**	−0.03	**0.79**				
Mat width	−0.02	**0.63**	−0.07	**0.84**	**0.77**			
Maximum frond order	**−0.20**	**0.54**	−0.06	**0.44**	**0.65**	**0.61**		
Maximum frond length	**−0.29**	**0.56**	−0.05	**0.42**	**0.61**	**0.59**	**0.90**	
Average rank	0.16	**−0.58**	0.07	**−0.47**	**−0.75**	**−0.62**	**−0.91**	**−0.90**

the two smaller reiterations at 50 m was unclear. The other fusion occurred on the right side of the main trunk between 55 and 60 m. The structure of this area of the crown was difficult to decipher because numerous trunks arose amidst thick accumulations of humus. The cambium was discontinuous on the left side of the main trunk between 60 and 70 m, forming a rotten hollow occupied by a dense thicket of ericaceous shrubs. One of the most interesting areas of the crown occurred on the right side of the main trunk between 50 and 55 m. Several trunks had snapped tops that became lodged in the crown along with a number of large branches. A surprising quantity of coarse woody debris had become incorporated into this region of the crown, forming "rafts" that continue to accumulate dead organic matter. Some of the dead wood in this area of the crown was fused with living branches and trunks.

Tree 4. Few redwoods have crowns as massive and sprawling as Tree 4, the 15th largest known living redwood (FIGURE 5), which is also known as Atlas Tree (Sawyer et al. 1999). The main trunk had negative taper between 50 and 57 m. Trunk diameter at 55 m was 3.2 m. Between 55 and 60 m, the main trunk was broken and gave rise to five major reiterations, including one that was centrally located within the crown. Fire scars were evident in the crown up to 70 m. The 21 reiterated trunks accounted for 14.9% of the tree's total wood volume (TABLE 1). The largest of these trunks was 1.7 m in basal diameter and 30.5 m tall. It gave rise to two other trunks. The larger of these emerged from the end of a huge branch and supported two other trunks as a forked top. A massive scar on the main trunk at ca. 58 m (not shown in FIGURE 5) was evidence of another trunk that apparently broke the top out of the 1.1 m diameter trunk emerging from the right side of the main trunk just below 50 m. Another trunk had since resprouted from this broken top. One reiteration was forked near the base, and both resulting trunks had broken tops (left side of FIGURE 5 ca. 60 m). Just above the fork, a fused branch linked the two trunks, and their diameters were greater above the fusion than below it (not shown in FIGURE 5). The taller of these trunks ended in a massive array of geotropic (i.e., steeply downsloping) branches that were covered by the largest *Polypodium scouleri* mat in the study. The shorter trunk gave rise to a sympodial trunk that was also broken. Most of the branches on Tree 4 were geotropic and hung down around the periphery of the crown like a gigantic curtain shading the interior of the tree (not shown in FIGURE 5), but several plagiotropic branches supported trunks. The largest of these emerged from the main trunk at 25 m. The trunk it supported was 0.7 m in basal diameter and 17.5 m tall.

Tree 5. This tree had 23 reiterated trunks, including one broken and three sympodial trunks (FIGURE 6), which accounted for 9.2% of its total wood volume (TABLE 1). The largest of these trunks was 1.4 m in basal diameter and 45.6 m tall. A 1.3 m diameter branch emerged from the right side of this trunk at ca. 42 m and gave rise to six other trunks, including one with foliage located as far as 10 m away from the main trunk. Several trunks arose from long branches coming off the main trunk. The two largest branches emerged from the left and right sides of the main trunk at 61 m and 59 m, respectively. The 1.6 m diameter branch on the left gave rise to three trunks, two of which were nearly identical except that one was completely dead. The 1.4 m diameter branch on the right gave rise to a trunk 0.8 m in basal diameter and 20.1 m tall. The top of the main trunk was a dead spire. Three trunks

TABLE 5. Summary of distribution and size variables for the epiphytic fern, *Polypodium scouleri,* on eight redwood trees. Mean values are listed along with one standard error in parentheses. Values for branch diameter and distance to main trunk are based on smaller sample sizes because 43 ferns did not grow on branches but grew directly on trunks. The maximum observed value of each variable is also listed. Maximum values with the same superscript letters came from the same fern mat.

Size class	Sample size	Height above ground m	Branch diameter cm	Distance to main trunk m
Maximum	—	90.0[a]	170.0[b]	8.0[c]
Huge	21	59.5 (2.54)	96.3 (9.69)	1.8 (0.38)
Large	50	60.4 (1.90)	53.1 (4.20)	1.7 (0.28)
Medium	70	60.2 (1.85)	33.5 (2.64)	2.0 (0.26)
Small	71	64.5 (1.64)	25.0 (1.72)	2.0 (0.18)

emerged from near the base of this spire amidst a welter of vascular epiphytes.

Tree 6. Tree 6 was the only redwood in the stand with an intact leader on its main trunk. This vigorous tree had 12 reiterated trunks (FIGURE 7) which accounted for 2.8% of its total wood volume (TABLE 1). All 12 trunks sprouted from branches. Two 0.7 m diameter trunks arose from 1.3 m diameter branches on the right side of the main trunk. Two 0.6 m diameter trunks arose from a 1.8 m diameter branch on the left side of the main trunk. This fern-covered branch, which was the largest in the study, gave rise to two smaller trunks, including one with foliage located as far as 8 m away from the main trunk. A large burl on the right side of the main trunk near the ground supported a perched soil occupied by vascular epiphytes.

Tree 7. In serious decline, Tree 7 had a main trunk that was dead and rotten above 70 m. Five of the 26 reiterated trunks (FIGURE 8), which accounted for 3.2% of the tree's total wood volume (TABLE 1), were entirely dead. The tops of three others were also dead. Nineteen of the trunks arose from five branches between 1.1 and 1.6 m in diameter. The largest branch gave rise to the tree's largest reiteration, a trunk 0.8 m in basal diameter and 17.8 m tall, as well as three other smaller trunks. All but two small trunks originated high in the crown; the main trunk had very little taper and was virtually devoid of branches below 60 m.

TABLE 6. Size class distribution of *Polypodium scouleri* fern mats (N = 212) by crown location in eight redwood trees. Values are expressed as % frequency within a size class.

Size class	Crown location: Crotch	Trunk	Branch
Huge	23.8	14.3	61.9
Large	22.0	6.0	72.0
Medium	4.3	12.9	82.8
Small	1.4	8.4	90.1

Tree 8. Known as the Del Norte Titan, Tree 8 is the largest known living redwood (Sawyer et al. 1999). There were three regions of negative taper on its main trunk: between 25 and 30 m, 50 and 55 m, and 60 and 65 m (FIGURE 9). The main trunk's diameter at 55 m was 3.7 m, but it quickly diminished to 2.4 m at 60 m after the emergence of three major reiterations. The 43 reiterated trunks accounted for 9.5% of the tree's total wood volume (TABLE 1). The largest of these trunks, which accounted for nearly half of the wood volume of all reiterations combined, was 1.6 m in basal diameter and 47.7 m tall. It was fused to the main trunk by a 1.4 m diameter branch at 45 m. This trunk and the main trunk were both thicker above the fused branch than below it. The fused branch gave rise to two other trunks, one of which supported a smaller trunk on the end of a branch. Several other small trunks arose from plagiotropic branches and supported foliage as far as 9 m away from the main trunk. A trunk 1.2 m in basal diameter and 27 m tall emerged from the main trunk at the same location as the largest reiterated trunk. The crotch formed by these three trunks held a layer of humus 2 m deep. Ten trunks had snapped tops. Half of these breaks were located on the left side of the main trunk between 59 and 67 m. This area of the crown was loaded with decaying wood, humus, and epiphytes. A trunk 1.5 m in basal diameter and 16.9 m tall arose from the right side of the main trunk at 60 m and supported 10 trunks of its own. Two 1 m diameter geotropic branches emerged from this trunk at ca. 62 m. These branches fused with the main trunk 10 m below their point of emergence (not shown in FIGURE 9). One of these massive branches gave rise to two small trunks (see right side of FIGURE 9 near *Vaccinium parvifolium*). Dozens of other geotropic branches occurred in

TABLE 5. Extended.

No. of fronds	Mat length cm	Mat width cm	Maximum frond order	Maximum frond length cm
2280[d]	820[d]	700[d]	19[d]	103[e]
367 (105.5)	279 (37.4)	180 (33.8)	15.8 (0.60)	74.7 (2.95)
138 (15.4)	165 (8.1)	79.0 (4.62)	11.8 (0.38)	57.7 (1.78)
45.8 (3.19)	81.2 (5.22)	41.0 (2.38)	8.3 (0.26)	41.2 (1.29)
14.7 (1.16)	22.1 (2.20)	15.8 (1.34)	3.7 (0.20)	19.3 (1.06)

the lower half of the crown (not shown in FIGURE 9), especially on the left side of the largest reiterated trunk. Some of these branches were 30 m long, flagelliform, and fusing with each other. The upper crown of Tree 8 was declining. The main trunk was rotten and hollow above 90 m, and there were several large dead branches above 80 m. Several smaller branches and a trunk arising from a branch near the top were, however, quite vigorous.

Epiphyte Distribution

Thirteen species of vascular epiphytes were found growing on the eight redwoods, including a spike-moss, three ferns, four shrubs, and five trees (TABLE 3). Only two species (*Polypodium scouleri* and *Vaccinium ovatum*) occurred on all eight trees. One species (*P. glycyrrhiza*) occurred on the majority of the trees, including all four trees in JSRSP. The other ten species occurred on three or fewer of the trees. The remaining analyses focused on the three dominant species: *P. scouleri, P. glycyrrhiza,* and *V. ovatum.*

Significant relationships were evident among measured variables for the dominant epiphytes. The evergreen fern, *Polypodium scouleri,* grew closer to the main trunk in the upper versus lower crowns; distance to main trunk was negatively correlated with height above ground (TABLE 4). The longest fronds were shorter in the upper versus lower crowns; maximum frond length was negatively correlated with height (TABLE 4). Overall, height above ground did not strongly affect *P. scouleri* fern mat size, although huge fern mats occurred, on average, lower in the crowns than the smaller fern mat size classes (TABLE 5). Larger fern mats grew on larger branches; branch diameter was positively correlated with size variables and negatively correlated with average rank (TABLE 4). Mean branch diameter steadily increased from smaller to larger fern mat size classes (TABLE 5). Fern mat size variables were highly intercorrelated with maximum frond order having the strongest correlation with average rank (TABLE 4). Mean values of each size variable steadily increased from smaller to larger size classes (TABLE 5). Fern mat size classes were significantly associated with crown locations ($P < 0.001$). Specifically, huge and large fern mats were more frequent in crotches than smaller fern mats; small and medium fern mats were more frequent on branches than larger fern mats (TABLE 6).

Polypodium glycyrrhiza was much less abundant than *P. scouleri,* and it grew considerably lower in the redwood crowns (compare TABLES 5 and 7). This deciduous fern was scarce on redwoods in PCRSP and only abundant on two of the redwoods in JSRSP (Trees 5 and 6). Overall, height above ground did not strongly affect *P. glycyrrhiza* fern mat size, although huge fern mats occurred, on average, 10 m lower in the crowns than small fern mats (TABLE 7). Larger fern mats grew on larger branches; branch diameter was negatively correlated with average rank (TABLE 8). Mean branch size increased from smaller to larger fern mat size classes (TABLE 7). All of the fern mat size variables were highly intercorrelated with maximum frond length having the strongest correlation with average rank (TABLE 8). Mean values of each size variable steadily increased from smaller to larger size classes (TABLE 7). All but one of the *P. glycyrrhiza* fern mats grew on branches (TABLE 12).

As with *Polypodium scouleri, Vaccinium ovatum* occurred on all eight redwoods, though it was only abundant on four of them (i.e., Trees 3, 5, 7, 8). Diameter of supporting branches, number of shrub stems, and maximum stem diameter were all positively correlated with height above ground (TABLE 9). These correlations (and the negative correlation between average rank and height above ground) were attributable to the presence of several huge- and large-size

TABLE 7. Summary of distribution and size variables for the epiphytic fern, *Polypodium glycyrrhiza,* on six redwood trees. Mean values are listed along with one standard error in parentheses. Values for branch diameter and distance to main trunk are based on smaller sample sizes because one fern did not grow on a branch but grew directly on a trunk. The maximum observed value of each variable also is listed. Maximum values with the same superscript letters came from the same fern mat.

Size class	Sample size	Height above ground m	Branch diameter cm	Distance to main trunk m
Maximum	—	68.2[a]	170.0[b]	6.6[c]
Huge	5	41.1 (4.54)	68.5 (11.02)	2.7 (0.56)
Large	9	47.1 (2.74)	54.4 (10.64)	1.5 (0.71)
Medium	13	46.8 (3.51)	51.6 (14.57)	2.6 (0.34)
Small	14	51.0 (3.36)	33.0 (6.71)	2.2 (0.47)

shrubs growing on thick branches high in the crown of Tree 7 (FIGURE 8). Larger shrubs grew on larger branches; branch diameter was positively correlated with all of the size variables and negatively correlated with average rank (TABLE 9). Mean branch diameter steadily increased from smaller to larger shrub size classes (TABLE 10). All of the shrub size variables were highly intercorrelated (TABLE 9). Mean values of each size variable steadily increased from smaller to larger size classes (TABLE 10). Shrub size classes were significantly associated with crown locations ($P < 0.05$). Specifically, larger shrubs were more frequent in crotches than smaller shrubs, huge shrubs were more frequent on trunks than smaller shrubs, and small shrubs were more frequent on branches than larger shrubs (TABLE 11).

The three dominant epiphyte species differed significantly in their crown locations ($P < 0.005$). Specifically, the *Polypodium* ferns were more frequent on branches than *Vaccinium ovatum,* which was more frequent on trunks than the ferns (TABLE 12). The prevalence of ferns on branches is evident in the crown diagrams (especially FIGURES 5 and 6) as constellations of epiphytes "floating" in space. Note that these diagrams only show branches that gave rise to reiterated trunks; no other branches, including those supporting the floating epiphytes, are shown. The prevalence of *V. ovatum* on trunks is most evident in FIGURES 4 and 9. Unlike the other epiphytes, which consistently grew from humus accumulations on bark surfaces, ericaceous shrubs such as *V. ovatum* often grew directly from decaying wood in tree crowns. Many shrubs grew on dead branches (33%) or from rotten hollows in trunks (13%) that lacked humus accumulations.

DISCUSSION

Tree Individuality

Large redwoods have complex crowns consisting of multiple reiterated trunks. Such crowns resemble forest stands more than individual trees. Trunk-to-trunk and trunk-to-branch fusions are common. Fusions presumably arise from wound responses, as sections of the crown abrade one another over time. Ultimately, water

TABLE 8. Summary of product-moment correlation coefficients (r) between distribution and size variables for the epiphytic fern, *Polypodium glycyrrhiza,* on six redwood trees. Statistically significant correlations ($P < 0.01$, $N = 41$) are highlighted in bold. Correlations for branch diameter are based on smaller sample sizes because one fern did not grow on a branch but directly on a trunk.

	Height above ground	Branch diameter	Distance to main trunk	No. of fronds	Mat length	Mat width	Maximum frond order	Maximum frond length
Branch diameter	0.15							
Distance to main trunk	−0.29	−0.27						
No. of fronds	−0.17	0.21	−0.06					
Mat length	−0.15	0.19	0.05	**0.82**				
Mat width	−0.24	0.38	−0.32	**0.62**	**0.43**			
Maximum frond order	−0.14	0.23	−0.06	**0.53**	**0.51**	**0.51**		
Maximum frond length	−0.31	0.36	−0.17	**0.48**	**0.44**	**0.65**	**0.80**	
Average rank	0.22	**−0.41**	0.13	**−0.80**	**−0.75**	**−0.78**	**−0.81**	**−0.84**

TABLE 7. Extended.

No. of fronds	Mat length cm	Mat width cm	Maximum frond order	Maximum frond length cm
145[d]	230[d]	140[e]	34[e]	55[f]
97.0 (14.11)	138 (24.8)	74.0 (16.91)	30.2 (1.02)	45.2 (2.37)
53.8 (8.30)	90.0 (8.37)	58.3 (8.50)	27.6 (1.49)	45.2 (2.09)
26.1 (3.02)	58.8 (6.32)	36.3 (2.54)	26.0 (1.24)	37.3 (2.51)
8.9 (1.53)	34.0 (6.19)	19.7 (3.34)	18.7 (1.09)	27.1 (1.52)

and nutrients are exchanged across these fusions (Sawyer et al. 1999), and tree hydraulic architecture becomes convoluted as resources are diverted from one section of the crown to another. Fusions may stabilize complex tree crowns, perhaps reducing damage during storms.

In addition to treefalls, severe storms induce "reiteration falls" when sections of complex crowns break in high winds. Detached trunks decimate underlying areas of the crown as they fall, and broken remnants of the crown frequently respond to these disturbances by reiteration. Young "stands" of reiterated trunks arise in these areas of the crown, and several cohorts of reiteration are often evident in the same tree. Broken trunks and branches do not always fall to the ground. Coarse woody debris is frequently retained in complex crowns, providing platforms for further debris accumulation. This debris and scars from torn out trunks and broken branches provide substrates for wood decay fungi.

Damaged areas of crowns are not the only sites of reiteration in large redwoods. Reiterated trunks frequently occur along trunks and branches lacking any signs of previous disturbances. Portions of the crown facing a canopy gap, which may be a stream corridor or the result of an adjacent treefall, are often abundantly reiterated. Thus, reiteration in redwood probably occurs in response to increased light availability. Regardless of the cause, reiteration leads to highly asymmetrical crowns in large redwoods. Individualized crown structure is a record of each redwood's responses to disturbances and fluctuating resource availability over many centuries, even millenia.

Crown Structure and Epiphyte Distribution

Large branches and crotches at the bases of reiterated trunks provide platforms for debris accumulation. Deep (up to 2 m) humus layers develop in such areas, especially in the lower crown. Tree foliage appears to initiate humus formation as it accumulates and decomposes. Once vascular epiphytes colonize the humus, they contribute substantially to its formation; rhizomes and roots of epiphytes are major components of crown humus (Bailey 1999, see also Ingram & Nadkarni 1993). Huge ferns mats and shrubs frequently occur in crotches with deep humus. The humus resource in large redwood crowns is exploited by a variety of epiphytic ferns, shrubs, and trees, including a number of

TABLE 9. Summary of product-moment correlation coefficients (r) between distribution and size variables for the epiphytic shrub, *Vaccinium ovatum,* on eight redwood trees. Statistically significant correlations ($P < 0.01$, $N = 92$) are highlighted in bold. Correlations for branch diameter are based on smaller sample sizes because 52 shrubs did not grow on branches; they grew directly on trunks.

	Height above ground	Branch diameter	Distance to main trunk	No. of shrub stems	Shrub length	Shrub width	Maximum stem diameter
Branch diameter	**0.28**						
Distance to main trunk	−0.18	−0.10					
No. of shrub stems	**0.28**	**0.54**	−0.24				
Shrub length	0.19	**0.55**	−0.21	**0.54**			
Shrub width	0.14	**0.63**	−0.14	**0.62**	**0.84**		
Maximum stem diameter	**0.28**	**0.54**	−0.20	**0.55**	**0.87**	**0.88**	
Average rank	**−0.28**	**−0.65**	0.12	**−0.67**	**−0.85**	**−0.88**	**−0.88**

TABLE 10. Summary of distribution and size variables for the epiphytic shrub, *Vaccinium ovatum,* by size classes on eight redwood trees. Mean values are listed along with one standard error in parentheses. Values for branch diameter and distance to main trunk are based on smaller sample sizes because 52 shrubs did not grow on branches but grew directly on trunks. The maximum observed value of each variable also is listed. Maximum values with the same superscript letters came from the same shrub.

Size class	Sample size	Height above ground m	Branch diameter cm	Distance to main trunk m	No. of stems	Shrub length cm	Shrub width cm	Maximum stem diameter mm
Maximum		90.0[a]	160.0[b]	5.5[c]	55[d]	560[e]	440[f]	63[f]
Huge	—	68.9 (2.06)	133 (3.5)	1.4 (0.35)	28.6 (4.78)	310 (37.3)	340 (23.6)	47.6 (3.90)
Large	22	64.9 (2.16)	88.9 (10.51)	2.1 (0.38)	12.4 (1.44)	192 (14.5)	194 (15.8)	28.0 (2.16)
Medium	31	63.5 (2.81)	66.9 (10.91)	2.1 (0.37)	5.3 (0.60)	94.2 (6.66)	95.6 (8.25)	15.9 (1.64)
Small	30	56.6 (2.05)	28.5 (4.49)	1.9 (0.51)	2.9 (0.40)	38.8 (4.32)	32.7 (3.30)	5.0 (0.50)

accidentally epiphytic species (e.g., *Lithocarpus densiflorus, Picea sitchensis, Polystichum munitum, Pseudotsuga menziesii, Rhamnus purshiana,* and *Ribes laxiflorum*) whose primary habitat is terrestrial. Thus, deep humus in large redwoods replicates conditions on the forest floor, presumably because of its high water-holding capacity (Veneklaas et al. 1990, Bohlman et al. 1995) and nutrient content (Putz & Holbrook 1989, Field et al. 1996).

Deep accumulations of humus hold large quantities of water. Like sponges, they fill up during the rainy season and discharge their stored water slowly during the dry season. Splash zones of sustained stemflow occurring beneath the deepest humus support aquatic algae and grazing mollusks on the bark throughout the year. Shallow humus accumulations receiving the enriched stemflow from such "canopy waterfalls" also harbor accidental epiphytes (e.g., the *Rhamnus purshiana* on Tree 4). The frequent presence of a lungless salamander, *Aneides ferreus,* in redwood crowns (pers. obs.) is further evidence that crown humus stores water throughout the year. These desiccation-sensitive salamanders actually breed in the humus beneath epiphytic ferns (Welsh & Wilson 1995).

In addition to humus, decaying wood is an important substrate for some vascular epiphytes in large redwood crowns. Ericaceous shrubs frequently colonize dead branches, snapped trunks, and scars from torn-out trunks. These epiphytes must rely on mycorrhizal fungi to supply water and nutrients from decaying wood (Lesica & Antibus 1990), because they frequently occur on substrates lacking accumulated humus. Ericaceous shrubs are an important resource for arboreal animals in redwood forests. In the spring, insects (e.g., bumblebees) pollinate the shrubs, which consistently produce abundant crops of berries in the fall (pers. obs.).

Tree-to-Tree Variation in Epiphyte Distribution

Complex crown structure clearly promotes humus accumulation and vascular epiphyte abundance in large redwoods. Much of the tree-to-tree variation in epiphyte distribution, however, cannot be attributed to difference in crown structure alone. Tree age, stand-level microclimate, tree health, and dispersal limitations also may influence epiphyte abundance in redwood forest canopies.

Trees 1 and 2 had highly reiterated crowns, but they supported far fewer vascular epiphytes than the other trees. Ages of the redwoods remain a mystery, although the much greater sizes of Trees 4, 5, 6, 7, and 8 suggest that they may be much older than Trees 1 or 2. If so, the greater abundance of vascular epiphytes on older

TABLE 11. Size class distribution of the shrub, *Vaccinium ovatum,* (N = 92) by crown location in eight redwood trees. Values are expressed as % frequency within a size class.

Size class	Crown location: Crotches	Trunks	Branches
Huge	22.2	55.6	22.2
Large	13.6	22.7	63.7
Medium	9.7	32.3	58.0
Small	0.0	20.0	80.0

TABLE 12. Distribution of dominant vascular epiphyte species by crown location in eight redwood trees. Values are expressed as % frequency within a species.

Species	Crown location: Crotch	Trunk	Branch
Polypodium glycyrrhiza	2.5	0.0	97.5
Polypodium scouleri	9.4	9.9	80.7
Vaccinium ovatum	8.7	28.3	63.0

trees may be partly attributable to the longer period available for accumulation of humus and epiphytes. Such a relationship between tree size/age and vascular epiphyte diversity has been documented in a Mexican cloud forest; larger/older trees supported a higher biomass and diversity of vascular epiphytes than smaller/younger trees (Hietz & Hietz-Seifert 1995a, 1995b).

Differences in tree age probably do not explain why Tree 3 supported so many more vascular epiphytes than Trees 1 and 2; all three trees were similar in size and grew in the same forest. Unlike Trees 1 and 2, tall *Picea sitchensis* trees harboring tremendous quantities of epiphytic bryophytes and ferns surrounded Tree 3. The high water-holding capacity of these thick epiphyte mats could have elevated crown-level humidity and promoted development of fern mats in Tree 3. Furthermore, Tree 3 had a large rotten hollow on the main trunk that supported a dense thicket of ericaceous shrubs. Decaying wood substrates were scarce in Trees 1 and 2, even though all three redwoods had vigorous, healthy crowns.

The tops of three redwoods (Trees 5, 7, and 8) were dead, and their main trunks contained numerous rotten hollows. Like Tree 3, ericaceous shrubs were prevalent on decaying wood in these redwoods. The least healthy redwood in the study (Tree 7) supported the largest quantity of ericaceous shrubs (3 huge-, 8 large-, 9 medium-size *Vaccinium ovatum* as well as 6 *V. parvifolium*). Tree 6, which grew adjacent to Trees 5, 7, and 8 in the same stand, had very little decaying wood, and ericaceous shrubs were relatively scarce in its healthy crown. Thus, tree health may influence vascular epiphyte distribution in redwood forest canopies regardless of tree age or stand-level microclimate. Specifically, tree decline may lead to an increasing abundance of ericaceous shrubs by providing decaying wood substrates.

In addition to tree age, stand-level microclimate, and tree health, dispersal limitations may be another source of tree-to-tree variation in epiphyte distribution. The best examples of disperal limitations occurred among the redwoods in JSRSP, where *Lithocarpus densiflorus* grew only on Tree 8, *Pseudotsuga menziesii* grew only on Tree 7, and *Selaginella oregana* grew only on Tree 5. Acorns of *L. densiflorus* were probably carried into the crown of Tree 8 by resident Douglas squirrels, who repeatedly chewed through my nylon cords! Animals, especially birds (e.g., band-tailed pigeons), also disperse berries of ericaceous shrubs. The epiphytic *P. menziesii* probably arrived as a wind-borne seed from a free-standing tree located more than 100 m away. Seeds of the other epiphytic conifers (*Picea sitchensis* and *Tsuga heterophylla*) are also wind-dispersed. The restriction of *S. oregana* to two branches of Tree 5 is more puzzling because this species produces wind-dispersed spores that should have been able to reach adjacent Trees 6, 7, and 8. This spike-moss also may disperse asexually via fragmentation of its pendulous sporophytes. It is one of the dominant epiphytes of temperate rain forests in some parts of the Pacific Northwest (e.g., Nadkarni 1984), reaching the southern limit of its distribution along the northern California coast (Wilken 1993). Insufficient rainfall may greatly limit its distribution in redwood forests farther south than JSRSP.

Rainfall and Fern Distribution

The most obvious epiphytic difference between the redwoods of PCRSP and JSRSP involves ferns in the genus *Polypodium.* Recall that the deciduous *P. glycyrrhiza* was scarce on redwoods in PCRSP and nearly restricted to lower crowns, whereas the evergreen *P. scouleri* was widespread on redwoods in both Parks. Unlike *P. scouleri,* which is limited to coastal areas with heavy fog drip, *P. glycyrrhiza* also occurs far inland in forests that experience severe summer droughts (Whitmore 1993). This species avoids drought by shedding its membranous leaves. In contrast, *P. scouleri* cannot withstand the severe droughts of inland forests, but leathery leaves and thicker rhizomes enable this species to tolerate the moderate dry seasons of coastal forests. These physiological traits may make *P. scouleri* more tolerant of desiccation during the wet season than *P. glycyrrhiza,* thus explaining the wider vertical distribution of *P. scouleri* in redwood forest canopies (Heitz & Briones 1998). Similarly, the scarcity of *P. glycyrrhiza* on redwoods in PCRSP may be attributed to this species' intolerance of dry episodes during the wet season. Such episodes are likely to be less frequent and less severe in JSRSP, which receives 30% more annual rainfall than PCRSP. Manipulative experiments are clearly needed to test these hypotheses.

Canopy Research in Redwood Forests

The first three years of redwood forest canopy research at Humboldt State University have revealed the complexity of large redwood crowns and the abundance of vascular epiphytes inhabiting them. We are studying crowns of tall *Picea sitchensis* as well. We have intensively sampled *Polypodium scouleri* on both redwood and *P. sitchensis* trees to estimate its biomass at the stand level (Bailey 1999). We are also sampling

nonvascular epiphytes and are finding a high biomass and diversity of lichens and bryophytes, especially on *P. sitchensis.* In addition to canopy structure and epiphyte distribution, we are investigating vertical gradients in microclimate (see Parker 1998), foliar water stress, and ecology of canopy-dwelling salamanders. Vital questions about redwood forest canopy biology remain unanswered, including many that can only be addressed with the aid of rope-based climbing techniques.

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